

THE
DIGESTION OF SUGARS IN HEALTH.

BY

W. G. AITCHISON ROBERTSON, M.D.,
D.Sc., F.R.C.P.E.

(Reprinted from the *Edinburgh Medical Journal* for September 1894.)

PRINTED BY OLIVER AND BOYD, EDINBURGH.

MDCCCXCIV.
c

THE DIGESTION OF SUGARS IN HEALTH.

IT is only within the last century that the consumption of cane sugar has become general; until a comparatively recent period its expense limited its use to the wealthy, while to the poor it was almost unknown. When a sweetening agent was desired, honey was commonly employed, and nearly every cottager kept his beehive, a custom which has now fallen into desuetude. As the price of cane sugar has fallen, so has its consumption increased. According to M'Culloch, the amount consumed in Great Britain in 1700 was 10,000 tons. In 1790 it reached 81,000 tons; although in 1808 the duty had risen to 27s. per cwt., 142,000 tons were used; while in 1864 there were imported 551,105 tons, a quantity equal to 30 lbs. per head. In 1891 the home consumption of raw and refined sugars was 1,352,676 tons, which is equivalent to an annual consumption of 80 lbs. per head.

Great Britain and America are the largest consumers of sugar. In other countries, as France, where the duty is higher, the consumption is proportionally less.

An article of diet so largely consumed merits as much attention from the physiologist and scientific physician as it has already received from the chemist.

The large employment of sugar in these times is no doubt a very important factor in the causation of dyspepsia. Our ancestors were much less troubled with indigestion than the present race, and the increase of this malady is commonly ascribed to increased civilisation and to the multiplication of sedentary occupations. Perhaps there is some truth in these ideas, but I have not found this disease more common among our hard brain workers than amongst our manual labourers. I believe the prevalence of indigestion mainly arises from the greater complexity of the diet now used, compared with the plain fare formerly consumed. Many dyspeptics have at an early period of their trouble to abandon saccharine foods, since they, soon after ingestion, cause much acidity, nausea, and heartburn. Why should this be so? Is cane sugar in itself so difficult of digestion, or is it because of its proneness to fermentative change that gastric disturbance is apt to arise? In what form is sugar absorbed into the blood? Is it as cane sugar, or is it as dextrose, lactose, or maltose? How

is cane sugar changed in digestion, and in what form is it absorbed ? These are the questions I shall endeavour to answer.

CHEMISTRY OF SUGARS.

1. *Cane Sugar*.—Let me briefly summarize some facts regarding the chemistry of sugars. When a solution of cane sugar or saccharose ($C_{12}H_{22}O_{11}$) is heated for a long time by itself, or for a short time in the presence of dilute mineral acid, it becomes "inverted." When yeast is added to a warm solution and a moderate temperature maintained, the cane sugar becomes first inverted and then suffers alcoholic fermentation. A solution of cane sugar is dextro-rotatory ; after inversion, however, the solution rotates the polarized ray to the left. During inversion cane sugar takes up a molecule of water, and then splits into equal parts of dextrose and laevulose. Petit maintains that these do not occur in equal proportions ; while Maumené believes that, in addition to these, inversion gives rise to other optically neutral bodies, and that the products are much more numerous than is generally believed.

The mineral acids are much more powerful and rapid in their inverting action than organic acids ; and of the inorganic, sulphuric acid is the most potent of all. The rapidity of inversion increases with the temperature to which the mixture of acid and sugar is raised.

2. *Dextrose*, glucose or grape sugar, is a crystallizable sugar. It is not so sweet as cane sugar, and is much less soluble in water. It rotates the plane of polarized light to the right.

3. *Laevulose*, or fructose, on the other hand, is a colourless syrup as sweet as cane sugar. It has also been obtained in colourless acicular crystals. It turns the plane of polarization to the left, but its specific rotatory power is far greater than that of glucose, and hence, even though these two sugars may exist in equal amounts in invert sugar, the plane of polarization lies to the left.

The suboxide of copper is not precipitated from an alkaline solution of tartrate of copper by boiling with a solution of pure cane sugar, unless the ebullition be carried on for a long time ; but if invert sugar be used, the copper oxide is at once reduced.

I. DIGESTION OF CANE SUGAR.

Action of Saliva on Cane Sugar.

It has been affirmed by some writers that saliva has an inversive action on cane sugar, while this is denied by others. I have sought to determine this point.

I have already stated that when a solution of cane sugar is heated alone it undergoes a slow inversion. To estimate the amount of this inversion I kept a 20 per cent. solution of pure cane sugar in a water-bath at a constant temperature of $38^{\circ} C.$

This solution was made by dissolving 200 grammes of pure dry cane sugar in distilled water and diluting to one litre. After being kept at this temperature for one hour, invert sugar amounting to 0·19 per cent. was produced. At the end of two hours this had increased to 0·252 per cent. This constitutes the control experiment, and shows the amount of inversion which a 20 per cent. solution of cane sugar undergoes after one and two hours' exposure to the normal temperature of the body.

To determine whether saliva had a greater inversive action on cane sugar than distilled water, I performed the following experiment:—

Equal volumes of human saliva and cane sugar solution (of strength equal to 40 per cent.) were mixed together to give a 20 per cent. solution of sugar. Several beakers containing this solution were placed in the water bath at 38° C. After thirty minutes no recognisable inversion had occurred. In forty-five minutes traces of invert sugar appeared, as shown by the reduction of copper oxide, and in one hour the invert sugar amounted to 0·2 per cent.; while in two hours it reached 0·27 per cent.

I. Cane Sugar, 20 per cent. at 38° C.	Invert Sugar.	
	In one hour.	In two hours.
1. Solution in distilled water,	0·19%	0·252%
2. " " saliva,	0·2	0·27
Difference,	·01	·018

The amount of inversion in presence of saliva is so nearly the same as in its absence, that we may safely conclude that normal human saliva has practically no influence in hastening or retarding the inversion of cane sugar. In fact, it seems to be perfectly passive in this respect. The results given in the above experiment were practically identical with those obtained in other experiments conducted on similar lines.

II. GASTRIC DIGESTION OF CANE SUGAR.

Cane sugar reaches the stomach unchanged. Does it undergo any digestion in this organ, or does it require any?

It is thought by some that cane sugar is absorbed unchanged, and that after its entrance into the portal vessels it is transformed into glucose through the agency of a ferment in the blood. Pavy is of opinion that it does not require to be changed by digestion to aid its absorption, but merely requires solution to enable it to pass into the bloodvessels. He is inclined to believe, however, that, as a matter of fact, it is at all events partially converted

into grape sugar before absorption from the alimentary canal. Bouchardat and Sandras state that, under the influence of the gastric juice and of the lining membranes, cane sugar is changed into invert sugar and lactic acid, and absorbed as such, and that it must undergo inversion before it can be absorbed and used up in the blood.

The gastric juice contains, besides pepsin, a milk-curdling ferment; and, according to Hammersten, there is also a lactic acid ferment that acts on milk sugar. But in opposition to this last statement, it is a fact that a pure solution of lactose does not undergo fermentation when acted on by the gastric juice.

The acidity of the gastric secretion is now universally believed to be due to free hydrochloric acid (as was first conclusively proved by Bidder and Schmidt), which amounts usually to 0·17 to 0·3 per cent. During the first stage of digestion, even though the contents of the stomach are acid, no free hydrochloric acid is found. The period when it appears varies in different individuals, and also varies with the diet. After breakfast it may not be found until 45–60 minutes have elapsed, while after a full dinner it is not evident until after the lapse of two hours.

Lactic acid is said by some to exist normally in gastric juice, though it never reaches an amount exceeding 1 per mille. Free hydrochloric or lactic acid can seldom be detected in the stomach of infants.

Of the total acidity which one estimates in the gastric juice during digestion, only a very small amount may be due to free hydrochloric acid, the greater part being caused by the presence of acetic, butyric, and lactic acids.

Action of Gastric Secretion on Cane Sugar.

Dalton, Leube, and others state that outside the body the gastric juice slowly changes cane sugar into glucose. Laborde, however, affirms that the invasive power of the gastric juice is less than that of a solution of hydrochloric acid of the same strength; but if a trace of hydrochloric acid be added to the gastric juice, its invasive power becomes greater than that of the dilute solution of hydrochloric acid alone. Leube makes an exactly opposite statement. Brown-Séquard, Schiff, and Smith say that cane sugar is inverted in the stomach, and Bourquelot thinks that it is partly inverted in the stomach, but that part passes directly into the blood and is there inverted by the carbonic acid. Hay could find no invasive ferment in the gastric mucous membrane. Frerichs states that cane sugar is not inverted even if left in the gastric juice for twelve to thirty-six hours; and Blondlot believes that the sugar undergoes no change while in the stomach. Richet found that unless he added hydrochloric acid to gastric juice, there was no inversion of cane sugar; and asserts, in explanation of this, that there is really no free hydrochloric acid in the gastric juice,

but that it is always combined with organic bodies. He states that under normal conditions the gastric juice in the stomach does not act on sugars.

According to Dalton, it cannot be shown that cane sugar undergoes any inversion during ordinary digestion, and that if taken along with other food there is probably no conversion of it into glucose in the stomach. Kühne and Hermann make similar statements, and Leube comes to the same conclusion. In the healthy stomach, he says, no inversion of cane sugar occurs; but if there be dilatation, then there is a considerable amount of inversion.

Inversion of Cane Sugar by Dilute Hydrochloric Acid.

To estimate the amount of inversion caused by a dilute acid in a solution of cane sugar, I performed the following experiments:—

To 100 c. c. of a 20 per cent. solution of cane sugar I added 0·2 c. c. of hydrochloric acid, and placed it in a water-bath at 38° C. After the lapse of one hour it was removed, and was found to contain 0·37 per cent. of invert sugar. After being heated thus for two hours, the invert sugar had increased to 0·45 per cent. Subtracting the amount of sugar which is inverted when the 20 per cent. cane sugar solution is heated alone, we find that after one hour the hydrochloric acid has caused an increased inversion of 0·18 per cent., and after two hours 0·198 per cent., or nearly $\frac{1}{5}$ th per cent. more.

Cane Sugar, 20 per cent. solution, at 38° C.	Invert Sugar.	
	In one hour.	In two hours.
1. Alone,	0·19 per cent.	0·252 per cent.
2. With 0·2 per cent. HCl,	0·37 „ „	0·45 „ „

This comparison shows that the presence of the acid in the solution of cane sugar nearly doubles the amount of invert sugar produced. At the end of two hours, only about $\frac{1}{5}$ th part of the cane sugar had undergone inversion in the presence of acid similar in amount to that of the gastric juice and at the temperature of the stomach.

Inversion of Cane Sugar by Gastric Secretion.

I then continued the experiment with the gastric secretion from a man with a perfectly normal digestion. At 8 A.M. he had breakfast of porridge and milk. At 10 A.M. I washed out his stomach thoroughly, and then injected three ounces of dilute *Liquor Carnis*

(*Caffyn*). (This extract has no reducing action on the alkaline solution of copper.) Introducing the stomach-tube one hour later, I drew off the gastric contents, and used this, after filtration, in the same way as I had formerly used the 0.2 per cent. solution of hydrochloric acid. The initial acidity of this fluid, estimated as free hydrochloric acid, amounted to 0.15 per cent. Into a vessel I placed 10 c. c. of each of the following, viz., the gastric fluid, water, and 20 per cent. solution of cane sugar. The acidity of this mixture was 0.05 per cent. hydrochloric acid, and the sugar in this mixture was reduced by the dilution to about 6.6 per cent. After having been kept for two hours at a temperature of 38° C., it contained 0.83 per cent. of invert sugar.

$$10 \text{ c. c. healthy gastric fluid} \quad \left. \begin{array}{l} \\ \\ \end{array} \right\} = 0.05 \text{ p. c.} = \left. \begin{array}{l} \text{Invert sugar after} \\ 2 \text{ hours} \\ 0.83 \text{ p. c.} \end{array} \right\}$$

$$10 \text{ c. c. water} \quad \left. \begin{array}{l} \\ \\ \end{array} \right\} = \text{HCl} \quad \left. \begin{array}{l} \\ \\ \end{array} \right\}$$

$$10 \text{ c. c. 20 p. c. cane sugar solution} \quad \left. \begin{array}{l} \\ \\ \end{array} \right\} = 0.83 \text{ p. c.}$$

To determine whether the gastric juice had a greater or less effect in inverting cane sugar than a pure acid solution of similar strength, I made a solution of hydrochloric acid of strength equal to that of this gastric fluid which I had just employed, and used it in place of the gastric secretion in a similar experiment. After being kept at a temperature of 38° C. for two hours, the invert sugar in the mixture amounted to 0.66 per cent.

$$10 \text{ c. c. solution of HCl} = 0.15 \text{ p. c.} \quad \left. \begin{array}{l} \\ \\ \end{array} \right\} = 0.05 \text{ p. c.} = \left. \begin{array}{l} \text{Invert sugar after} \\ 2 \text{ hours} \\ 0.66 \text{ p. c.} \end{array} \right\}$$

$$10 \text{ c. c. water} \quad \left. \begin{array}{l} \\ \\ \end{array} \right\} = \text{HCl} \quad \left. \begin{array}{l} \\ \\ \end{array} \right\}$$

$$10 \text{ c. c. 20 p. c. cane sugar solution} \quad \left. \begin{array}{l} \\ \\ \end{array} \right\} = 0.66 \text{ p. c.}$$

The amount of invert sugar formed in the latter experiment being only 0.66 per cent., as compared with 0.83 per cent. when diluted gastric juice was used, seems to demonstrate that healthy gastric juice has a greater inverting power than a solution of hydrochloric acid of similar strength, and thus corroborates Leube's statement that sugar inversion is less rapid and less energetic with a pure acid solution than with gastric juice, but is opposed to what Laborde affirms, that the inverting power of gastric juice is less than that of hydrochloric acid diluted to the same degree of acidity.

It has been definitely stated that there is a sugar-inverting ferment in the gastric secretion. To determine whether the inverting action of the acid is aided by such a ferment, I proceeded as follows:—

I mixed equal volumes of healthy gastric fluid, water, and 20 per cent. solution of cane sugar, and then carefully neutralized the acidity with potassium hydrate. I used specially prepared and very sensitive litmus paper to test the reaction. After keeping the mixture at 38° C. for one hour, there was no trace of invert sugar; after two hours, a faint trace of invert sugar had appeared, but too minute for quantitative estimation.

10 c. c. healthy gastric fluid	Carefully neutralized	Invert sugar after 2 hours— mere trace.
10 c. c. water		
10 c. c. 20 p. c. solution of cane sugar		

Therefore, when the acidity of gastric juice is neutralized no inversion of cane sugar occurs. I conclude that there is practically no sugar-inverting ferment in gastric juice, otherwise an appreciable amount of invert sugar would have been formed in the above mentioned experiment.

It is evident from these experiments that the acidity of the gastric juice is the only factor in causing inversion of cane sugar.

The preceding experiments were performed in the laboratory with fresh human gastric juice. I desired to investigate the changes, if any, which cane sugar undergoes *in the stomach*. I experimented on a healthy man by the following method:—At 8 A.M. he had breakfast of porridge and milk. Two hours later I washed out his stomach thoroughly by means of a syphon elastic tube, and then poured 250 c. c. of a warm 20 per cent. solution of pure cane sugar into the stomach, the patient being thus quite ignorant of the nature of the fluid which was introduced. At intervals of from half an hour to two hours after the injection I passed the stomach tube and removed some of the gastric contents. Each sample of the gastric fluid so obtained was measured and filtered, and the reducing sugar in it estimated by Fehling's solution. The total acidity was estimated by titration with a centi-normal solution of caustic soda, and expressed in terms of anhydrous hydrochloric acid. I did not estimate the amount of free hydrochloric acid, as it was unnecessary, but I always tested for the presence of inorganic (of which hydrochloric is the chief) and organic acids qualitatively.

Having estimated the acidity and the amount of invert sugar present, I then inverted the unchanged cane sugar in a definite amount of the gastric fluid by heating it for two hours with a few drops of dilute sulphuric acid (1 c. c. ordinary acid to 9 c. c. water). At the end of this time, any cane sugar present in the fluid had undergone complete inversion.

Normal Healthy Gastric Digestion.

In the first place, it was necessary to investigate the general character of this healthy man's gastric secretion; so, after washing out his stomach, he was allowed to eat quickly 250 c. c. of cooked minced steak.

(1.) One hour later, 60 c. c. of muddy dark brownish-red fluid were drawn off. This contained much swollen and softened muscular tissue; fat in very small masses; total acidity was equal to 0.211 per cent. hydrochloric acid; inorganic acids were present, and a large quantity of organic acid; peptones were present in large amount, and fibrin soon dissolved in it on adding a trace of hydrochloric acid.

(2.) After two hours, 35 c. c. of turbid brown fluid were drawn off. The muscular tissue was further broken down, and fat occurred in larger masses; the total acidity was equal to 0.185 per cent. hydrochloric acid; inorganic acid was present in large amount, and organic acid also. The peptone reaction was hardly so marked as in the first case, and fibrin, as before, was quickly dissolved.

As another control experiment, I washed out this healthy man's stomach and then injected 250 c. c. of normal saline solution (=0.7 per cent. Na Cl.)

(1.) After one hour I drew off 140 c. c. slightly turbid fluid. Total acidity was equal to 0.075 per cent. hydrochloric acid; inorganic acids were alone present. Polariscopic gave $-1^{\circ}2$. It contained no substance that had any reducing effect on Fehling's solution. After acidifying this fluid and heating it in a water-bath for two hours there was no chemical change.

(2.) After two hours 60 c. c. were drawn off. The acidity was equal to 0.178 per cent. hydrochloric acid; inorganic acids were alone present; the polariscope showed $-0^{\circ}7$, and the fluid contained no reducing substance.

In this case the polariscope shows a rotation of the polarized ray to the left, although no sugar was present. All proteids are laevo-rotatory, and there are peptones in the gastric fluid after injecting saline solution.

This, then, is the character of the gastric fluid with which we have to deal in the case of this healthy digestion.

Normal Gastric Digestion of Cane Sugar.

In each experiment 250 c. c. of 20 per cent. cane sugar solution were injected into the empty stomach, and samples of this were drawn off at varying intervals. The following Table gives the results of these observations:—

Series.	Time during which Cane Sugar was in Stomach.	Number of Cubic Centimetres drawn off.	Total Acidity as HCl per cent.	Presence of Inorganic Acids.	Presence of Organic Acids.	Per cent of Invert Sugar formed in Stomach.	Total Amount of Reducing Sugar when Inverted outside.	Remarks.
	Minutes							
I.	30	160	0.09	+	+	0.25	2.44	No lactic acid.
II.	60	36.5	0.124	+	+	0.81	1.28	Trace of lactic acid.
III.	60	90	0.115	+	+	0.42	1.7	Trace of lactic acid.
IV.	90	40	0.125	+	+	0.13	0.495	...
V.	120	41	0.1428	++	+	0.68	0.934	Trace of lactic acid.
VI.	120	85	0.185	++	+	0.41	0.65	No lactic acid

These experiments show—

1. That inversion of cane sugar really takes place in the healthy stomach.

2. That as digestion proceeds the proportion of invert sugar to the whole sugar increases.
3. That the amount of invert sugar formed is proportional to the acidity of the gastric juice.
4. That the total amount of sugar diminishes as digestion proceeds.

III. NORMAL GASTRIC DIGESTION OF INVERT SUGAR.

I prepared the invert sugar in the following manner:—One litre of the 20 per cent. solution of pure dry cane sugar was placed in a flask, and to it was added one cubic centimetre of dilute sulphuric acid (1 c. c. ordinary commercial acid to 9 c. c. water). The flask was then placed in a water-bath, and heated for two hours at a temperature of 170°–180° F. After allowing it to cool, it was made up to its original volume by adding water. This 20 per cent. solution of invert sugar gives a rotation of -10° by the polariscope of Zeiss.

I proceeded to experiment with this in the same way as I had done with the cane sugar solution, introducing 250 c. c. of the 20 per cent. solution of invert sugar into the previously emptied stomach, and passing the syphon tube after an interval of one and two hours, and withdrawing some of the gastric contents.

Digestion of Invert Sugar in the Healthy Stomach.

Series.	Numbers of c. c. withdrawn after being 1 or 2 hours in Stomach.		Total acidity as per cent. HCl		Per cent. Invert Sugar remaining in fluid withdrawn.		Remarks.
	1 hour.	2 hours.	1 hour.	2 hours.	1 hour.	2 hours.	
I.	100	24	0.176	·1276	1·8	1·25	
II.	100	0	0.172	0	2·77	0	Stomach empty at second hour.
III.	100	66	0.229	0.164	2·27	0·44	No lactic acid, but other acids present.
IV.	120	11	0.182	0.175	3·3	0	No lactic acid.
V.	75	0	0.156	0	4·5	0	No lactic acid. Stomach empty at second hour.

If we compare this table with that of the digestion of cane sugar, we see that there is a very great difference as regards the behaviour of these two sugars in the stomach.

First. As regards the quantity of fluid in the stomach. In the case of cane sugar there was always much fluid in the stomach, even after the lapse of two hours. In no case was it less than 86 c. c. It is very different with invert sugar, however. When it was injected much fluid could be withdrawn up to the end of the first hour, but after two hours the stomach was entirely or almost empty, as only in one or two cases could a few cubic centimetres be extracted. The stomach therefore becomes quickly emptied of invert sugar.

Second. If we compare the columns in the table after one and two hours, we see what a reduction has taken place in the amount of sugar. What has become of this invert sugar? It must either have been rapidly absorbed through the walls of the stomach, or have been passed on through the pylorus into the duodenum. Probably both of these processes go on at the same time.

IV. INTESTINAL DIGESTION OF CANE SUGAR.

Neither the biliary nor the pancreatic secretions seem to have any inversive action on cane sugar. Béchamp thought that the pancreas had a slight inversive action, but the change which he saw was in all probability due to bacteria causing decomposition, and not to any ferment.

The mucous membrane of the small intestine, however, secretes a ferment which has been named "invertin," and which causes cane sugar to become hydrated and split up into glucose and lactose. This fermentative action of the succus entericus was first described by Claud Bernard. The ferment can be isolated, and then acts on cane sugar, but much more slowly than when in contact with the mucous membrane of the small intestine. Bernard found that it was present in every part of the small, but not in the large intestine. Sir William Roberts also describes this ferment, and has extracted it from the small intestine of the pig, fowl, and hare. It will not, he finds, pass through a filter, and its inversive action is very slow, usually requiring two hours at 38° C. before any reduction of copper takes place. Hoppe-Seyler does not think that this is a true ferment of the intestinal mucous membrane, but believes that it is one introduced from without, and Busch could not find that cane sugar underwent any change during its stay in the bowels. Hay, however, found this ferment constantly present in every part of the small intestine of the foetus, and in such a case it could not have been introduced from without. Demant has also described this *invertin* ferment, and also a diastatic one in the small intestine, but he finds that they require to act on the sugar or starch for four or five hours before any inversion of sugar or conversion of starch occurs. Brown and Heron have also studied this question, and find that a watery infusion of the small intestine possessed no inversive action on cane sugar, but when they used the dried and powdered mucous

membrane of the small intestine they found a marked inversion. They say that this property lies chiefly in the agminated glands of the small intestine.

To observe for myself whether this inversive ferment was active, and in what localities it was to be found, I made the following experiments:—

A healthy young rabbit was starved for thirty-six hours. It then received a full meal, and was killed two hours subsequently, so that the various digestive processes might then be in full activity. I had previously prepared a 5 per cent. solution of pure cane sugar, and having placed 50 c. c. into separate flasks, I heated all to 38° C. Having carefully but gently washed the contents from the alimentary canal of the animal with a stream of normal salt solution, I then placed 5 grammes of different parts of the intestinal tract and other organs into separate flasks containing the sugar solution, and kept them at 38° C. for two hours. They were then allowed to cool, and the amount of inversion (if any) which had taken place estimated. The following Table shows what tissues were employed, and is arranged in the order of greatest inversive power of the tissues.

Rabbit: 5 grms. each of—	Per cent. Invert Sugar formed.
1. Lower part of small intestine,	1.14
2. Upper part of small intestine,961
3. Vermiform appendix, lower part,362
4. Liver,297
5. Vermiform appendix, upper part,233
6. Central part of stomach,233
7. Pancreas,217
8. Large intestine,148
9. Cardiac end of stomach,144
10. Pyloric end of stomach,143
11. Spleen,133
12. Thyroid,084
13. Salivary glands,068
14. Muscle,065
15. Kidney,062
16. Oesophagus,061
17. Bile,	0

This certainly shows that there is a very decided inversive action in the small intestine of the rabbit, and also an action to a very much smaller extent with the other parts of the digestive tract.

I then performed exactly the same experiments with tissues of

an infant which had lived three days, and had been fed on the breast during this period. The salivary glands were too small to be worth while removing. The following Table is also arranged in the order of the greatest inversive power of the tissues.

Infant: 5 grms. each of—	Per cent. Invert Sugar formed.
1. Small intestine,543
2. Large intestine,384
3. Stomach, central part,032
4. Oesophagus,012
5. Stomach, pyloric end,	0
6. Stomach, cardiac end,	0
7. Pancreas,	0
8. Liver,	0
9. Thyroid,	0
10. Kidney,	0
11. Bile,	0
12. Thymus,	0
13. Spleen,	0

A comparison of these two tables shows that the chief inversive action, both in the infant and in the rabbit, lies in the small intestine. It is a relatively powerful ferment, and, distributed as it is throughout the whole extent of the small intestine, will easily suffice to invert all the assimilable cane sugar which is ingested.

Recapitulating, therefore, we have seen that cane sugar is—

1. Unchanged by saliva.
2. Inverted to a certain small extent in the stomach, depending entirely on the degree and nature of the acidity of gastric fluid.
3. Inverted completely in the small intestine by the action of the ferment "invertin."